

# The Selection Mosaic and Diversifying Coevolution between Crossbills and Lodgepole Pine

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**ABSTRACT:** Asymmetrical competition determines which of two seed predators drives the evolution of lodgepole pine (*Pinus contorta* ssp. *latifolia*) cones. Red squirrels (*Tamiasciurus hudsonicus*) are effective preemptive competitors in lodgepole pine forests so that red crossbills (*Loxia curvirostra*) are uncommon and selection from *Tamiasciurus* drives cone evolution. When *Tamiasciurus* are absent, crossbills increase in abundance and coevolve in an evolutionary arms race with pine. Similarly, *Tamiasciurus* alters the evolutionary trajectories of large-seeded pines, many of which rely on birds (Corvidae) for their seed dispersal. Populations therefore exhibit a selection mosaic with coevolutionary hot spots. In the coevolutionary hot spots, divergent selection on crossbills potentially leads to reproductive isolation and speciation. This results in a subsequent reduction in the geographic mosaic but diversifies the adaptive landscape on which crossbills have radiated. Thus, divergent selection is a double-edged sword. Divergent selection is critical in creating a selection mosaic but erodes the selection mosaic when it promotes reproductive isolation and speciation.

**Keywords:** coevolution, competition, divergent selection, geographic mosaic, predator-prey, speciation.

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Interspecific interactions are seldom uniform throughout a species' range. Consequently, selection on a given species shifts geographically, such as when an interaction switches from mutualistic to antagonistic (e.g., Thompson and Pellmyr 1992; Thompson 1997, 1999, in this issue). This variation in interspecific interactions among populations causes divergent selection between populations and a geographic mosaic of coevolution (Thompson 1994, 1997, 1999, in this issue). Although divergent selection is integral to the geographic mosaic of coevolution, divergent selection eventually erodes the geographic mosaic if speciation occurs.

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Here I test whether a dominant competitor acts to impede a coevolutionary arms race between a subordinate competitor and their shared prey. I will show that Rocky Mountain lodgepole pine (*Pinus contorta* ssp. *latifolia*) cone structure is influenced primarily by selection exerted by red squirrels (*Tamiasciurus hudsonicus*). However, when *Tamiasciurus* (the dominant competitor) are absent, red crossbills (*Loxia curvirostra*) increase in abundance and coevolve in an evolutionary arms race with pine. A result is that populations exhibit a selection mosaic with coevolutionary hot spots. In some situations, gene flow or population movements lead to mismatches between the traits of interacting populations, as predicted (Thompson 1994, 1997, 1999, in this issue; Burdon and Thrall 1999, in this issue; Parker 1999, in this issue). But in the coevolutionary hot spots, divergent selection is apparently promoting reproductive isolation and speciation, which reduces the geographic mosaic but diversifies the adaptive landscape on which crossbills have radiated (Benkman 1993a). The selection mosaic may often lead to divergent, multifarious selection in different parts of a species' range, which are the conditions, even with gene flow, that can quickly lead to reproductive isolation and speciation (Rice and Hostert 1993; McPeck 1996).

## Study System: Crossbills, Squirrels, and Lodgepole Pine

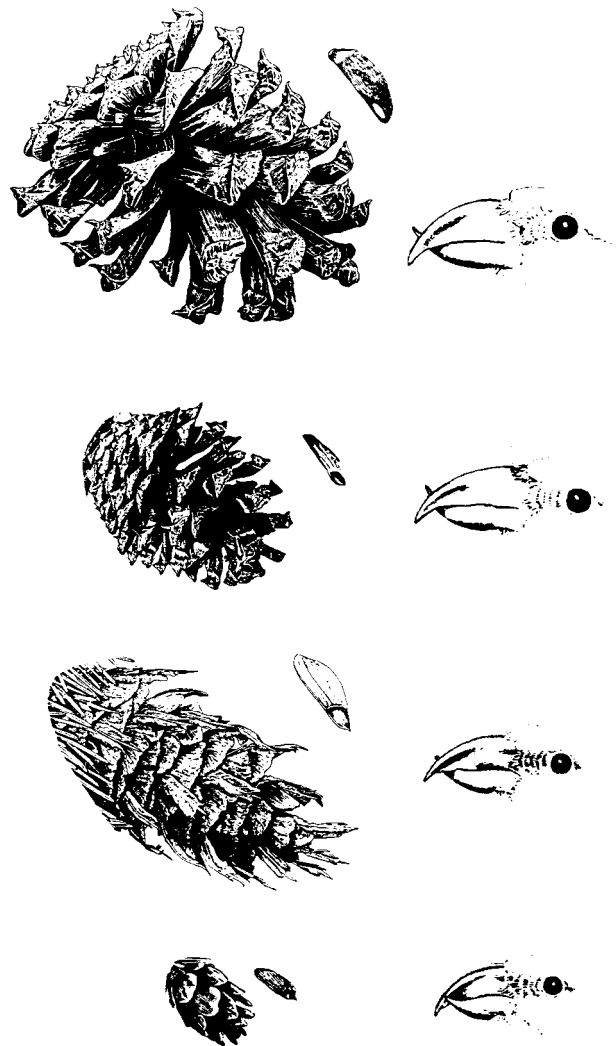
An ideal study system for examining the geographic mosaic of coevolution is a recent adaptive radiation where the processes involved in population subdivision and divergence may still be active. Equally important is that the costs and benefits of changes in traits affecting species interactions can be quantified. Red crossbills (*Loxia curvirostra* complex) in North America represent such a system (Benkman 1989b, 1993a, 1993b; Groth 1993). There is a clear and direct functional link between the morphology and ecology of crossbills and their food resources, seeds in conifer cones. For example, feeding performance influences crossbill habitat and conifer use, movements, and breeding behavior (Benkman 1987b, 1989a, 1990, 1992), and bill size and cone structure determine feeding

performance (Benkman 1987a, 1993a; Benkman and Miller 1996). Thus, simple measures of feeding performance provide a currency to assess the impact of changes in cone structure.

The diversity of crossbills is related to the structure and diversity of conifer cones and seeds (fig. 1; see also fig. 10). The eight putative species of red crossbills in North America are very similar in coloration and general appearance, but they differ in body size, bill size (Groth 1993), and palate structure (Benkman 1993a). These differences in bill structure are correlated with the different species of conifers on which each crossbill specializes (Benkman 1989b, 1993a). Indeed, the predicted optimal bill sizes and husking groove widths for foraging on the different species of conifers (fig. 1) are similar to the averages of the different species of crossbills (Benkman 1993a; Benkman and Miller 1996). The diversity of crossbills, therefore, is dependent on the diversity of conifer cones and seeds, with certain characteristics allowing crossbills to specialize (Benkman 1993a; see also Thompson 1994).

An unanswered question is whether crossbills have affected the evolution of conifers. If so, then crossbills may have coevolved with conifers and potentially influenced both crossbill and conifer diversification. I begin addressing the question of coevolution by focusing on the geographic pattern of the interactions of red crossbills and red squirrels as seed predators and selective agents on Rocky Mountain lodgepole pine. The effect of *Tamiasciurus* needs to be considered because they are important and well-known selective agents on conifer cone structure in North America (Smith 1970; Elliott 1974, 1988; Linhart 1978; Benkman 1989b, 1995a).

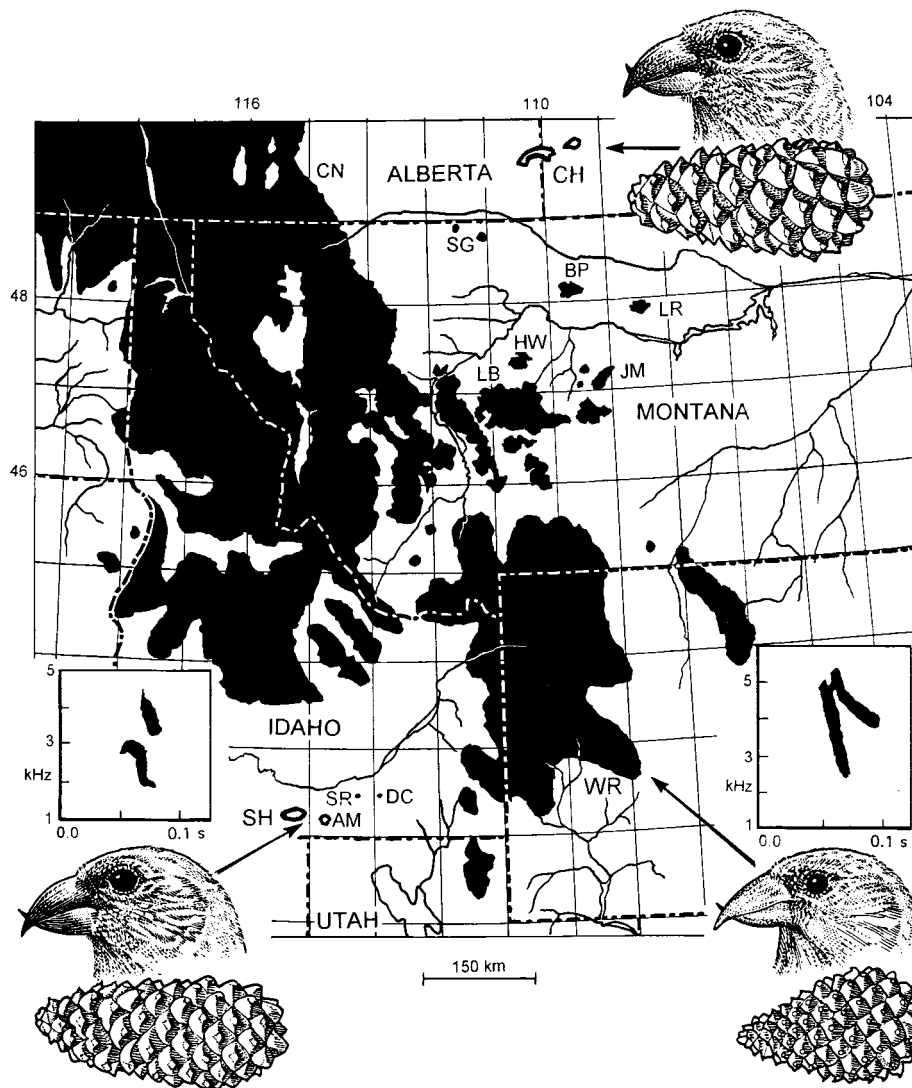
Rocky Mountain lodgepole pine is appropriate for study for several reasons. First, one species of red crossbill (type 5 of Groth 1993) is specialized for foraging on seeds in the cones of Rocky Mountain lodgepole pine (Benkman 1993a; Benkman and Miller 1996). Second, the evolutionary effect of *Tamiasciurus* on lodgepole pine is well documented (Smith 1970). Third, crossbills and *Tamiasciurus* are the main seed predators; no insect feeds regularly on seeds in Rocky Mountain lodgepole pinecones (Smith 1975). Fourth, isolated mountain ranges lack *Tamiasciurus* and differ in area and distance from extensive areas of lodgepole pine and therefore their ability to support resident populations of crossbills (fig. 2). In addition, four of the isolated areas support two distinct populations of red crossbills (fig. 2). Fifth, these lodgepole pine forests are of postglacial origin or have become isolated from the Rocky Mountain forests following the last glacial period so that any changes are recent and processes involved in divergence may still be active.



**Figure 1:** A schematic of four different forms or call types of red crossbills (Groth 1993) and the cones on which each crossbill specializes (from top to bottom: ponderosa pine *Pinus ponderosa* ssp. *scopulorum*, lodgepole pine *Pinus contorta* ssp. *latifolia*, Douglas-fir *Pseudotsuga menziesii* ssp. *menziesii*, western hemlock *Tsuga heterophylla* [reproduced from Sudworth 1917, 1967]). The bills are drawn to relative scale and so are the cones, but bills are drawn about 1.5 times larger compared with the cones.

#### *Tamiasciurus* as a Preemptive Competitor

*Tamiasciurus* harvest many cones and cache them in mid-dens soon after the seeds mature in late summer and early autumn but before the cone scales begin opening (Smith 1968, 1970, 1981; Findley 1969; Benkman et al. 1984). Seeds in these cached cones provide the main winter food for *Tamiasciurus* and are unavailable to crossbills (Smith 1968, 1970, 1981). Crossbills forage for most of the year on cones left on the tree (Benkman 1987b, 1990, 1992)



**Figure 2:** The distribution of lodgepole pine (black) (modified from Critchfield and Little 1966), the location of study sites, and representative crossbills and cones in the Rocky Mountains, the Cypress Hills, the South Hills, and the Albion Mountains. The crossbills and cones are drawn to relative scale. Representative sonograms of flight calls are shown for the South Hills crossbill (left) and the Rocky Mountain lodgepole pine crossbill (right). The acronyms for each site, whether *Tamiasciurus* are present (+), absent (-), or recently introduced (i), and for isolated areas, the estimated area of lodgepole pine forest in square kilometers, follow: Albion Mountains (AM, -, 16–20); Bear's Paw Mountains (BP, -, 40); Cypress Hills (CH, i, 73 [West Plateau] and 7 [Centre Block]); Crow's Nest Pass (CN, +); Deep Creek Mountains (DC, +, 6); Highwood Mountains (HW, +, 96); Sweetgrass Hills (SG, -, 3 [West Butte] and 4 [East Butte]); Little Belt Mountains (LB, +) Little Rocky Mountains (LR, -, 17); South Hills (SH, -, 70); Sublett Range (SR, +, 5–7); Wind River Range (WR, +). One Rocky Mountain study site not shown was near the Twin Lakes, Colorado, approximately 650 km south-southeast of the Wind River Range site.

unharvested by *Tamiasciurus*. Thus, crossbills have little impact on the cone availability for *Tamiasciurus*, but the early removal of cones by *Tamiasciurus* has the potential to reduce seed availability for crossbills (Smith and Balda 1979). A strong competitive effect was found in Newfoundland, where the formerly common Newfoundland crossbill (*Loxia curvirostra* ssp. *percna*) declined following

the introduction and subsequent increase of *Tamiasciurus* (Benkman 1989b, 1993b; Pimm 1990).

I used data from 10-min point counts to determine whether crossbills are less abundant in forests occupied by *Tamiasciurus*. I only analyze the numbers of crossbills perched within 100 m of the observer because these crossbills used the local habitat, whereas those, for example,

flying over might not. Point counts were conducted in mature and old-growth lodgepole pine forests in 12 national forests in western Montana and northern Idaho (between mid-May and mid-July 1994–1996; R. Hutto, unpublished data) where *Tamiasciurus* were present and in the South Hills of southern Idaho (June 1998) where *Tamiasciurus* were absent. Most lodgepole pine trees had serotinous cones in both areas (Lotan 1975; C. W. Benkman, personal observation); serotinous cones remain closed until sufficient heat melts the resinous bonds holding the cone scales together (Johnson and Gutsell 1993).

Crossbills were over 20 times more abundant (Wilcoxon's rank sum test,  $Z = 19.1$ ,  $P < .0001$ ) in the South Hills (mean = 3.30 red crossbills/point count, SE = 0.41,  $n = 50$  point counts) where *Tamiasciurus* were absent than in the Rocky Mountains (mean = 0.15, SE = 0.04,  $n = 785$  point counts). The high abundance of crossbills in areas without *Tamiasciurus* is consistent with historical accounts of crossbills in Newfoundland (see Benkman 1989b, 1993b) and the Cypress Hills, Canada (Godfrey 1950; W. E. Godfrey, personal communication, 1987) where *Tamiasciurus* were absent until recent introductions.

*Tamiasciurus* should have a greater selective impact than crossbills on lodgepole pinecones for several reasons. First, *Tamiasciurus* harvest most of the cones (see, e.g., Elliott 1988) before crossbills harvest many seeds. Consequently, selection by crossbills is limited to the subset of cones left by *Tamiasciurus*. Second, selection by an uncommon predator is likely to be trivial in the evolution of a prey compared with selection from common predators (Bell 1997). *Tamiasciurus* undoubtedly consume many more seeds than crossbills. I cannot compare crossbill point count data to density estimates of *Tamiasciurus*; however, the average density of 1.3 *Tamiasciurus* per hectare in Rocky Mountain lodgepole pine forests (Gurnell 1984) is likely much greater than that of crossbills in the same forests (the densities of mammals are generally about an order of magnitude greater than those of similarly sized birds; Brown 1995). In addition, *Tamiasciurus* have an estimated field metabolic rate that is about 2.7 times greater than that estimated for a crossbill (based on allometric relationships in Nagy 1987 and assuming body masses of 218 g [Smith 1968] and 32 g, respectively). Moreover, this approach underestimates the relative energy demands of *Tamiasciurus* because their basal metabolic rate is nearly two times greater than that predicted for their body mass (Smith 1968).

#### *Tamiasciurus* as Selective Agents on Cone Structure

*Tamiasciurus* are important selective agents on lodgepole pinecones (Smith 1970; Elliott 1974, 1988). To quantify this further, I gathered three cones, recently cut by *Tamiasciurus*, from the base of 30 lodgepole pine trees on 30

different *Tamiasciurus* territories in the West Plateau of the Cypress Hills in September 1994. These trees generally had few cones remaining on their branches (see Elliott 1988). I compared these cones with three cones gathered from trees that were near the harvested tree and from which few cones had been harvested by *Tamiasciurus*. Because *Tamiasciurus* are more selective of cone traits with increasing distance from the midden (Elliott 1988), I selected pairs of trees (>12 m tall) that were approximately equidistant from the nearest midden. The following cone and seed traits were measured: closed cone length, maximum width of closed cones, the thickness at the distal end of six scales in the middle of the distal third of the cone and in the middle of the proximal third of the cone (the six scales were selected approximately equidistant around the cone), cone mass with seeds removed, number of seeds and number of full seeds (i.e., filled with kernel) per cone, and the individual masses of five seeds and the masses of their kernels from each cone. All length measurements were made to the nearest 0.01 mm with digital calipers. All mass measurements were made to the nearest 0.1 mg with a digital scale after the cones and seeds were oven-dried at 60°–70°C for over 2 d.

*Tamiasciurus* preferentially harvested cones that were narrow at the base compared with their length, had over 1.5 times more full seeds, and had a higher ratio of kernel mass to cone mass (table 1). These results are similar to those in earlier studies (Smith 1968, 1970; Elliott 1974, 1988) and are easily interpreted. Narrower cones are easier for *Tamiasciurus* to harvest and to bite through the scales to the underlying seeds (Smith 1970; Elliott 1974, 1988). *Tamiasciurus* have higher feeding rates on cones with more seeds and with a higher ratio of kernel mass to cone mass (Smith 1970; Elliott 1988). Other traits, such as cone length, width, and mass, and average kernel mass, did not differ significantly between *Tamiasciurus*-harvested trees and nearby unharvested trees (table 1).

Whether lodgepole pine will evolve from the presence and absence of selection by *Tamiasciurus* requires that cone traits are heritable. Many of the measured lodgepole pinecone traits are heritable:  $H^2$  (broad sense heritability) = 0.53 for cone length, 0.30 for cone width, 0.25 for cone mass, 0.43 for seed mass, and 0.37 for the number of seeds per cone (T. S. Kimbrell et al., unpublished manuscript).

#### Geographic Variation in Lodgepole Pinecone Structure

If *Tamiasciurus* are important selective agents on cone structure, then cones should be narrower, have more seeds, and have a higher ratio of kernel mass to cone mass in areas without *Tamiasciurus* than in areas with *Tamiasciurus*. I gathered cones from at least 22 trees from all the

**Table 1:** Cone and seed traits ( $\bar{X} \pm \text{SEM}$ ) from adjacent trees that were either relatively unharvested or harvested by *Tamiasciurus* introduced into the Cypress Hills

Trait	Unharvested tree	Harvested tree	$P^a$
Cone length (mm)	45.77 $\pm$ .82	47.76 $\pm$ .84	.099
Cone width (mm)	27.54 $\pm$ .43	27.23 $\pm$ .47	.62
Cone width/length (mm)	.605 $\pm$ .010	.570 $\pm$ .006	.007 <sup>b</sup>
Proximal scale thickness (mm)	2.72 $\pm$ .08	2.61 $\pm$ .05	.19
Distal scale thickness (mm)	2.71 $\pm$ .05	2.60 $\pm$ .04	.12
Cone mass (gm)	9.188 $\pm$ .295	9.501 $\pm$ .405	.54
Number of full seeds/cone	28.80 $\pm$ 1.89	44.62 $\pm$ 2.33	<.0001
Individual kernel mass (mg)	4.35 $\pm$ .18	4.46 $\pm$ .15	.59
Kernel mass/cone mass (mg)	.013 $\pm$ .0008	.021 $\pm$ .0010	<.0001

Note: Three cones were sampled from each of 30 unharvested and 30 *Tamiasciurus*-harvested trees. All analyses were based on the mean for each tree.

<sup>a</sup>  $P$  values are from paired  $t$ -tests (two-tailed).

<sup>b</sup> Based on a Wilcoxon signed-rank test.

study sites (see fig. 2) to characterize variation in cone structure in relation to the presence of *Tamiasciurus*. Three cones were measured, as described earlier, from each tree. The means and variances of all the measured traits usually leveled off at sample sizes of 10 to 15 trees and always by 20 trees (based on random subsamples of 38 trees from the Little Rocky Mountains). I used the correlation matrix from the ln-transformed means of seven cone traits for each tree in a principal component analysis (table 2) to characterize cone variation. Principal component analyses were done with JMP version 3.2.1 for the Macintosh (SAS 1997). I used the number of seeds per cone rather than the number of filled seeds in this analysis because the number of filled seeds, but not the number of seeds, is influenced by the frequency of outcrossed pollen, which varies depending on, for example, stand density (Smith et al. 1988).

Much of the variation in cones between trees is related to general changes in size (table 2). As PC1 increases, cones get larger, and scale thickness increases especially for distal scales, and the size and total number of seeds increases (table 2). As PC2 increases, cones become wider compared with length, basal scales especially become thicker, and cones have fewer seeds (table 2). Variation among sites in terms of PC1 and PC2 is mostly along a diagonal (fig. 3), with smaller values of PC1 and larger values of PC2 associated with sites having *Tamiasciurus*.

If *Tamiasciurus* is the main selective agent, then defenses against *Tamiasciurus* should decline in their absence. Changes in cone structure therefore should parallel the

line connecting the average cones from trees *Tamiasciurus* avoided to those harvested (solid line in fig. 3B). Some variation between sites with and without *Tamiasciurus* occurs as predicted (fig. 3B). That is, PC2 decreases and PC1 increases in the absence of *Tamiasciurus*. In further support of the hypothesis that defenses directed toward *Tamiasciurus* have declined, *Tamiasciurus* introduced in the Cypress Hills have territories that average only about one-fourth (0.237 ha; Hurly and Lourie 1997) of those in Rocky Mountain lodgepole pine forests (0.907 ha; Smith 1968). The small territories and high squirrel density in the Cypress Hills are unlikely to be the result of other factors such as fewer predators, because correlative data and food addition experiments show that food supply limits densities of *Tamiasciurus* (Smith 1968, 1970, 1981; Kemp and Keith 1970; Sullivan and Sullivan 1982; Sullivan 1990; Klenner and Krebs 1991).

Nevertheless, most of the variation in cone structure among sites occurs along PC1 (fig. 3B). This result suggests that some factor(s) other than just selection by *Tamiasciurus* is important in determining the evolution of cone structure. I will now consider three possible explanations.

One hypothesis for the intersite variation is that cone size and other traits vary in response to fire frequency or other abiotic factors. For example, nonserotinous lodgepole pinecones tend to have more seeds per cone than serotinous cones (Muir and Lotan 1985). Such an explanation is unlikely for three reasons. First, strong similarities exist between the floristic composition and physiognomy of the lodgepole pine forests in the Rocky Mountains and

**Table 2:** The principal component loadings of the seven cone traits (ln transformed) describing cone structure and the amount of variation explained by the first two principal components

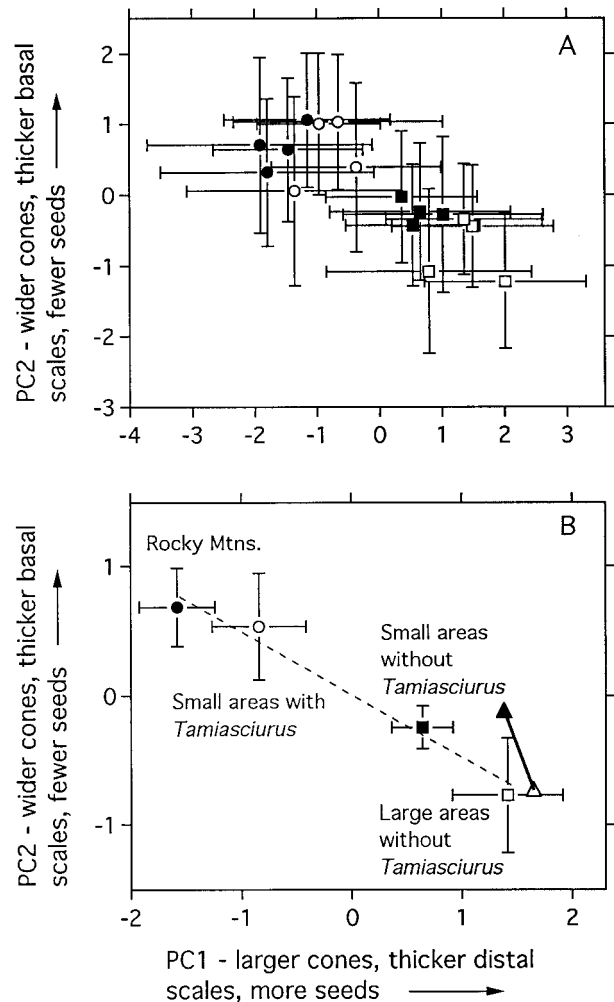
	PC1	PC2
Length	.462	-.225
Width	.431	.267
Cone mass	.494	.041
Number of seeds	.307	-.433
Individual seed mass	.382	-.183
Distal scale thickness	.327	.291
Proximal scale thickness	.100	.755
Percentage of variation explained	49.3	20.5

Cypress Hills (La Roi and Hnatiuk 1980). Second, cones are similar from lodgepole pine populations occupying a variety of environments (see Pfister and Daubenmire 1975) throughout the Rocky Mountains from the Yukon to Colorado, yet they are very different from cones in the Cypress Hills (Wheeler and Guries 1982*b*), South Hills, and Albion Mountains. Finally, most trees from all sites had serotinous cones (only serotinous cones were sampled), which implies roughly similar fire histories (Muir and Lotan 1985) and stand characteristics (Brown 1975).

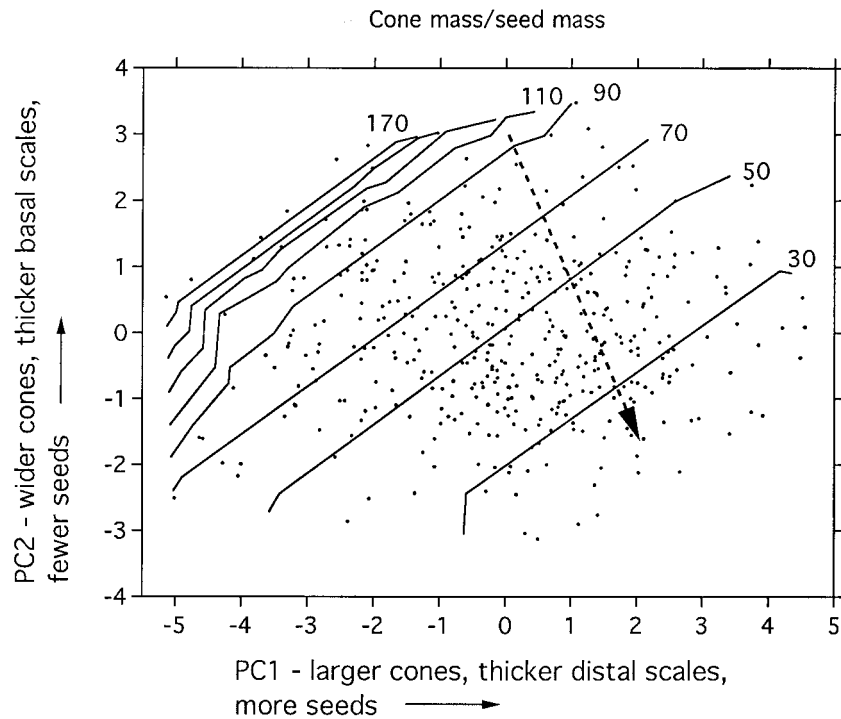
A second hypothesis is that without *Tamiasciurus*, trees that allocate proportionately more resources to seeds relative to cone mass should be favored (Smith 1970; Benkman 1995*a*). I used projection pursuit approximation (Schluter and Nychka 1994) to estimate the ratio of cone mass to seed mass (average individual seed mass times the number of seeds per cone) in relation to the first two principal components describing cone structure variation (fig. 4). One projection was used to estimate the contours in all projection pursuit approximations; two to four projections did not provide a significantly better fit. If trees were selected to maximize the proportion of resources allocated to seeds, then the ratio of cone mass to seed mass should decline in the absence of *Tamiasciurus*. The direction in which this ratio decreases is more similar to that predicted just from relaxation of selection from *Tamiasciurus* (arrow in fig. 4) than to the observed changes in cone structure (fig. 3). This suggests that the observed changes in cone structure are not simply the result of either relaxation of selection by *Tamiasciurus* or selection for allocating proportionately more resources to seeds. A third hypothesis is that crossbills exert strong selection on cone structure when *Tamiasciurus* are absent.

#### Cone Evolution in Response to Crossbills

Selection by crossbills could result in pines increasing their cone defenses directed at crossbills or maximizing the ben-



**Figure 3:** Variation in cone structure among study sites in relation to the first two principal components of seven cone and seed traits. The mean ( $\pm$ SD) values for each site (A) and all sites for a given combination of area and presence or absence of *Tamiasciurus* (B). The symbols in A correspond to the same area types designated in B. The dashed line represents the best-fit least squares regression ( $PC2 = 0.006 - 0.495[PC1]$ ,  $r^2 = 0.98$ ,  $df = 2$ ,  $P = .01$ ). The solid line connects the two triangles: the open triangle represents the mean values of cones harvested by *Tamiasciurus*, whereas the filled triangle represents the mean values of cones left unharvested by *Tamiasciurus* (table 1); these values were estimated using the eigenvectors in the principal component analysis in A. The symbols in A from left to right represent the following study sites (number of trees in parentheses): Twin Lakes (23), Crow's Nest Pass (28), Wind River Range (24), Sublett Range (22), Little Belt Mountains (22), Highwood Mountains (25), Judith Mountains (25), Deep Creek Mountains (26), East Butte of the Sweetgrass Hills (25), Little Rocky Mountains (38), West Butte of the Sweetgrass Hills (27), Albion Mountains (25), Bear's Paw Mountains (24), Centre Block of the Cypress Hills (30), Western Plateau of the Cypress Hills (29), and South Hills (29).



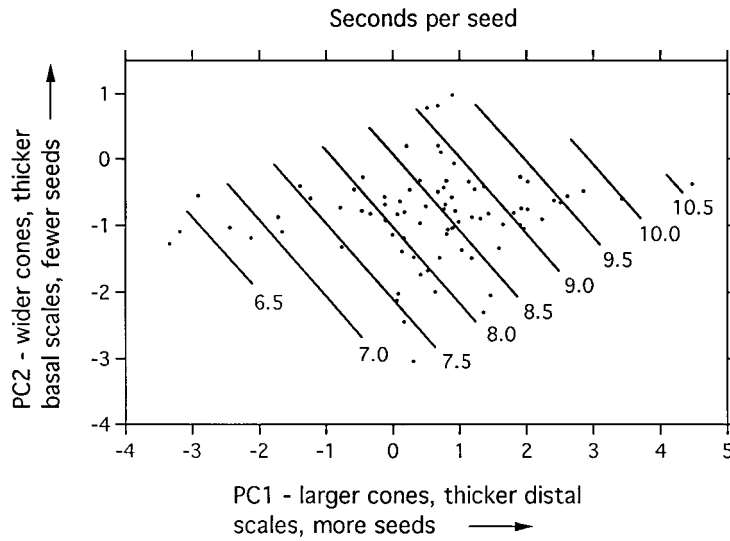
**Figure 4:** The estimated contours (solid lines) for the ratio of cone mass (mg) to total seed mass (mg) in relation to the first two principal components of seven cone and seed traits as in figure 3. The dashed line (it is the solid line from fig. 3, but extended) and arrow represent the predicted change in cone structure in the absence of selection by *Tamiasciurus*. Each point represents a different tree used to estimate the surface ( $n = 420$  trees).

efits of cone defenses relative to their costs. To test these two hypotheses, I begin by analyzing crossbill feeding performance in relation to variation in the first two principal components of cone variation. I use feeding performance (time per seed) as a measure of the form of this selection because crossbills maximize feeding rates when foraging (Benkman 1987b, 1989b) and therefore avoid trees where time per seed is high. Foraging experiments were conducted between January 15 and March 17, 1998, with eight captive red crossbills (type 2 of Groth 1993; their average bill depth was 9.39 mm, SE = 0.13, which represents a bill depth intermediate between lodgepole pine crossbills in the Rocky Mountains [9.32 mm, SE = 0.05,  $n = 32$  birds] and crossbills in the South Hills [9.89 mm, SE = 0.04,  $n = 49$  birds]). Each crossbill was timed removing and husking 10 seeds, beginning after the first seed was eaten (see Benkman and Miller 1996 for additional details on experimental protocol and aviary setup), from one cone from each of 82 trees (a total of 6,500 seeds). Cones were given to crossbills in random order with respect to values of PC1 and PC2. I assumed that the PC scores for the cones used in the foraging experiments were the same as those estimated for the tree as previously. This assumption is reasonable given that within-tree variance in cone traits

is significantly smaller than the between-tree variance (Smith 1968; Elliott 1974).

I used projection pursuit approximation to estimate the average number of seconds spent foraging per seed in relation to the first two principal components describing cone structure variation (fig. 5). If changes in cone structure were solely to deter crossbills (i.e., increased time spent foraging), then the first two principal components of cone structure should increase in areas where crossbills were potentially the main selective agent. This result was not found (fig. 3).

The other hypothesis is that trees have evolved to maximize the effectiveness of resources allocated to defense (i.e., the ratio of benefits to costs is maximized), instead of simply increasing defenses. Benefits can be equated to increases in time spent foraging by crossbills, whereas costs can be equated to increases in the proportion of resources allocated to cone relative to seed. Figure 6 shows the estimated ratio of benefit to cost in relation to variation in the first two principal components of cone structure using projection pursuit approximation. It follows that as selection from *Tamiasciurus* is replaced by selection by crossbills, cones should evolve toward the lower right of figure 6. As predicted, the trajectory of change (dashed line in

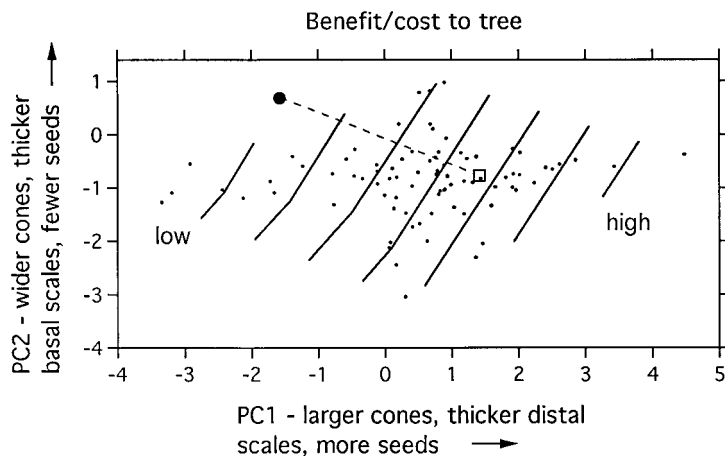


**Figure 5:** The estimated contours (*solid lines*) for the number of seconds crossbills required to remove a seed from a cone in relation to the first two principal components of seven cone and seed traits as in figure 3. Each point represents a different tree used to estimate the surface ( $n = 82$  trees).

fig. 6) ascends the contours of increasing benefits to costs. This shows that the change in cone structure in the absence of *Tamiasciurus* can be accounted for by selection by crossbills. Trees have maximized the effectiveness of resources (cone) allocated to defense against crossbills and have not simply lost defenses directed at *Tamiasciurus* or just increased defenses against crossbills.

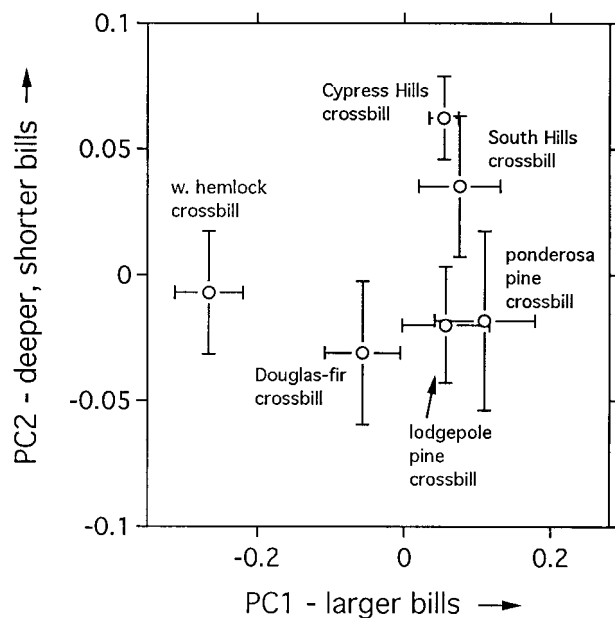
**Coevolution Leads to Divergent Selection on Crossbills**

Crossbills have evolved stouter bills in the Cypress Hills and in the South Hills and Albion Mountains (hereafter just South Hills) (figs. 2, 7) in apparent response to the increase in putative defenses directed at crossbills. The larger cones and thicker scales likely deter crossbills from



**Figure 6:** The estimated contours (*solid lines*) for the benefit-to-cost ratio to the tree (low to high) in relation to the first two principal components of cone and seed traits as in figure 3 (see text). The filled circle represents the overall mean values for sites from the Rocky Mountains (*Tamiasciurus* present), and the open square represents the overall mean values for sites where *Tamiasciurus* are absent and crossbills are resident. Each point represents a different tree used to estimate the surface ( $n = 82$  trees).





**Figure 7:** The mean ( $\pm$ SD) principal component scores for three bill measurements of six different forms of red crossbills. The covariance matrix from the ln-transformed measurements were used in the principal component analysis. The three bill measurements (and the loadings on the first two principal components) were upper mandible length (0.631,  $-0.182$ ), lower mandible length (0.632,  $-0.443$ ), and bill depth (0.450, 0.878) (see Benkman 1993a). The first and second principal components explained 91.5% and 5.7% of the variation, respectively. Sample sizes were 44 western hemlock crossbills, 12 Douglas-fir crossbills, 27 lodgepole pine crossbills, 61 ponderosa pine crossbills, 10 Cypress Hills crossbills, and 48 South Hills crossbills. All crossbills were alive when measured except the Cypress Hills crossbills.

prying apart the closed cone scales, especially toward the distal half of the cone (fig. 2), where most of the seeds occur and where crossbills usually forage on lodgepole pine. Presumably, large, stout-billed crossbills are more efficient on cones from the Cypress Hills and the South Hills than are the smaller-billed lodgepole pine crossbills from the Rocky Mountains. These differences in bill structure are likely heritable because pronounced environmental effects have not been noted when crossbills have been raised on atypical foods (Benkman 1993a), and bill size is generally highly heritable in birds (Boag and van Noordwijk 1987; Grant and Grant 1989).

I tested whether there should be selection for deeper bills by measuring the feeding rates of 14 red crossbills (type 2 of Groth 1993). As earlier, each crossbill was timed extracting (prying time) and husking 10 seeds from each of 10 cones from trees whose cones typified those from the Cypress Hills and the South Hills. I estimated feeding efficiency in terms of minimizing the time required to meet daily energy expenditures as done earlier (Benkman 1993a;

Benkman and Miller 1996). I also analyzed prying time separately because bill size (depth) is closely related to prying time but not seed husking time (Benkman 1993a).

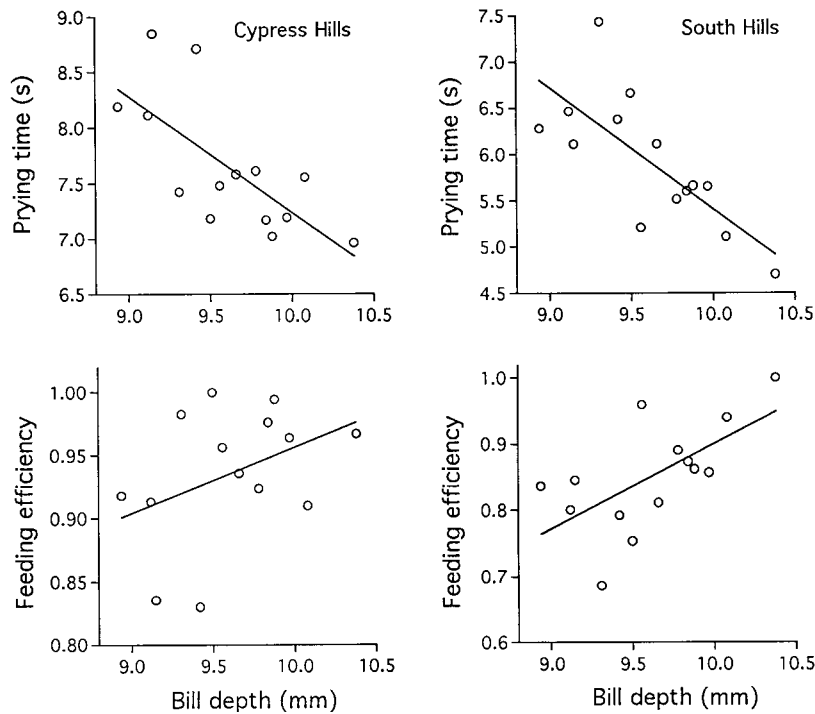
Selection for foraging on cones from the Cypress Hills and the South Hills should favor a deep bill. Time to remove a seed from a cone (i.e., prying time) decreases and feeding efficiency increases with increases in bill depth to about 10.0 mm in both the Cypress Hills and the South Hills (fig. 8). Whether crossbills in the Cypress Hills (mean depth = 10.04 mm, SE = 0.05,  $n = 10$  study skins) or the South Hills (mean depth = 9.89 mm) have evolved the optimal bill depth for foraging on their respective cones is unknown; additional feeding experiments are needed on South Hills crossbills with sufficiently large bills to detect where feeding efficiency levels off.

Divergent selection is suggested from comparisons of crossbill feeding efficiency (fig. 9). The optimal bill depth for foraging on lodgepole pinecones from the Rocky Mountains is about 9.3 mm, with feeding efficiency declining with further increases in bill depth (fig. 9; Benkman 1993a; Benkman and Miller 1996). In contrast, feeding efficiency on cones from the South Hills increases as bill depth increases above 9.3 mm. This result suggests that coevolution between crossbills and lodgepole pine in the South Hills (and in the Cypress Hills) leads to directional selection favoring increased bill depth. The result is divergent selection between crossbills in the Rocky Mountains and crossbills in both the Cypress Hills and the South Hills.

### The Geographic Mosaic

The stable annual cone crops of Rocky Mountain lodgepole pine (Smith 1970; Smith and Balda 1979) enable *Tamiasciurus* to attain densities that allow them to remove most of the cones in early fall during most years (Smith 1968, 1970; Hurly and Lourie 1997). Thus, *Tamiasciurus* are effective preemptive competitors (Smith and Balda 1979). In these forests crossbills are uncommon, and *Tamiasciurus* drive cone structure evolution (Smith 1970; Elliott 1974, 1988), coevolving with lodgepole pine (Smith 1970; see also Lindsay 1986).

*Tamiasciurus* are widespread throughout the range of lodgepole pine (Smith 1968, 1970), which presumably accounts for the similar structure of lodgepole pinecones from the Yukon to Colorado (see Wheeler and Guries 1982b). Here crossbills have adapted to the average cone (Benkman 1993a; Benkman and Miller 1996) but apparently have little impact on lodgepole pinecone evolution. On the periphery of the distribution of lodgepole pine occur isolated mountains and plateaus that lack *Tamiasciurus* (fig. 2). Here lodgepole pine increases the effectiveness of its defenses directed at crossbills in response



**Figure 8:** The mean prying time per seed and estimated foraging efficiencies for 14 red crossbills foraging on cones from the Cypress Hills (*left*) and South Hills (*right*) in relation to bill depth. Bill depth was measured with digital calipers at the anterior end of the nares to the nearest 0.01 mm. Five to seven measurements per bird were used to estimate bill depth. The solid lines represent best-fit least squares linear regressions (clockwise from top left:  $Y = 17.74 - 1.05X$ ,  $r^2 = 0.50$ ,  $df = 12$ ,  $P = .004$ ;  $Y = 18.49 - 1.31X$ ,  $r^2 = 0.56$ ,  $df = 12$ ,  $P = .002$ ;  $Y = -0.38 + 0.13X$ ,  $r^2 = 0.40$ ,  $df = 12$ ,  $P = .016$ ;  $Y = 0.44 + 0.05X$ ,  $r^2 = 0.16$ ,  $df = 12$ ,  $P = .16$ ).

to selection from crossbills (fig. 6). In ranges large enough to support resident crossbills, crossbills are common and coevolve with pines. This situation occurs in the South Hills and also in the Cypress Hills until the introduction of *Tamiasciurus* in 1950 (Newsome and Dix 1968).

Most other conifers produce more variable annual cone crops so that during large cone crops large fractions of the cones remain unharvested by *Tamiasciurus* (Smith and Balda 1979). Crossbills search for and accumulate in areas with large cone crops (Newton 1972; Benkman 1987*b*, 1992). As a result, crossbills are less affected by competition from *Tamiasciurus* when annual cone crops vary greatly than when cone crops are stable. The stability of lodgepole pinecone crops, therefore, enables *Tamiasciurus* to dominate crossbills in terms of both access to seeds and the evolutionary effects on cone structure. However, stable cone crops also allow crossbills to coevolve with lodgepole pine when *Tamiasciurus* are absent. The result is a selection mosaic with scattered hot spots of coevolution between crossbills and pines. This represents the first two parts of Thompson's (1994, 1997, 1999, in this issue) three-part coevolutionary hypothesis. The third part concerns trait remixing.

### Selection, Area, and Trait Remixing

Thompson (1994, 1997, 1999, in this issue) argues that differential gene flow among interacting populations causes traits of interacting species to be well matched in some communities but not in others. Here I argue that factors that affect the stability of a crossbill population (i.e., size of the area), possibly pollen flow (area's isolation), and the form of selection influence whether traits of interacting populations of crossbills and lodgepole pine are well matched. These are analogous to factors that affect local adaptation or trait matching of parasites to hosts (e.g., population turnover, gene flow, and level of virulence, respectively; Lively 1999, in this issue; Parker 1999, in this issue).

Crossbills track patterns of seed availability (Benkman 1987*b*, 1992). When annual cone crops fluctuate, crossbills are nomadic (Newton 1972; Benkman 1987*b*, 1992), but when cone crops are stable, crossbills are sedentary (Senar et al. 1993). The annual cone crops of Rocky Mountain lodgepole pine are nearly uniform (Smith and Balda 1979), so crossbills can be sedentary. However, some minimal area of lodgepole pine is also necessary to support a res-

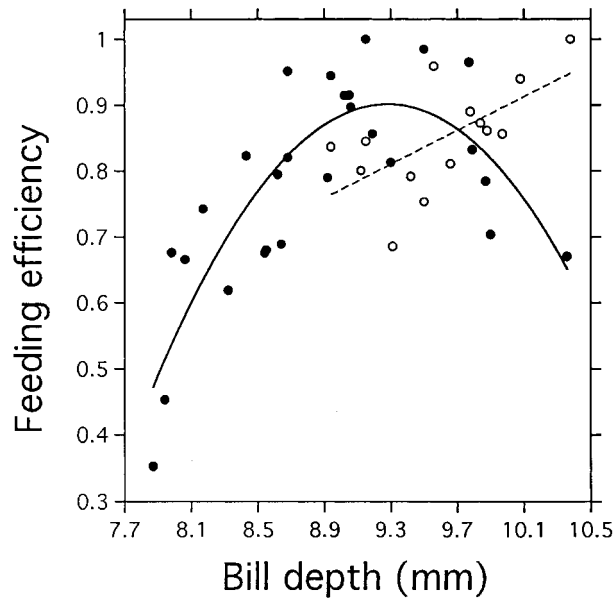


Figure 9: The estimated foraging efficiencies of red crossbills foraging on cones from the Rocky Mountains (filled circles, solid curve:  $Y = -17.63 + 3.99X - 0.22X^2$ ,  $r^2 = 0.69$ ,  $df = 24$ ,  $P < .0001$ ; data from Benkman 1993a; Benkman and Miller 1996) and the South Hills (open circles, dashed line) in relation to bill depth. All crossbills with bill depths  $>9.1$  mm were ponderosa pine crossbills.

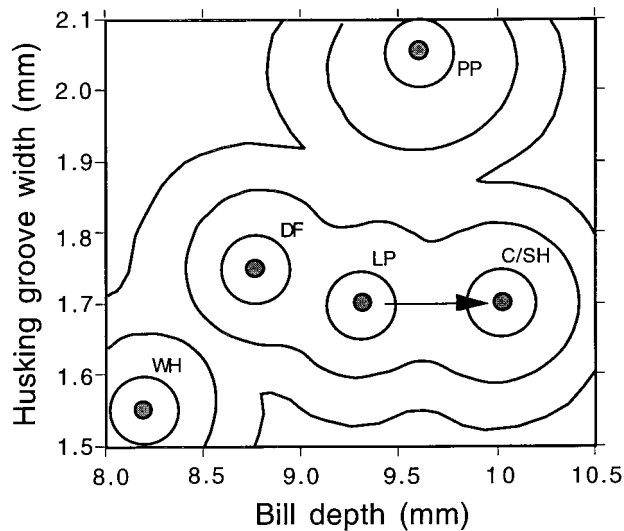
ident population. Smaller areas support only transient crossbills, so local matching of traits between crossbills and pines is unlikely. For example, the small forests of the Sweetgrass Hills (a total of about 7 km<sup>2</sup> of lodgepole pine on two buttes 27 km apart; Thompson and Kuijt 1976; fig. 2) do not support a resident crossbill population, but without *Tamiasciurus*, defenses directed at crossbills have increased (fig. 3). When crossbills from the Rocky Mountains are present, they exert selection on cone structure, but their small bills do not match the cones. Similarly, small areas with *Tamiasciurus* (e.g., Sublett Range and Deep Creek Mountains) and downwind from areas where crossbills are coevolving (e.g., Albion Mountains and South Hills) (fig. 2) are better defended against crossbills but not as well defended against *Tamiasciurus* (fig. 3), perhaps because of pollen flow. In terms of both *Tamiasciurus* and transient crossbills, the traits of the pines in the Sublett Range and Deep Creek Mountains are mismatched. If pollen flow has caused this mismatch, then isolated ranges with *Tamiasciurus* downwind from the Rocky Mountains (e.g., Highwood Mountains [HM] and Judith Mountains [JM]; fig. 2) should have cones similar to those in the Rocky Mountains. Cones in the Highwood and Judith Mountains are similar to those in the Rocky Mountains (fig. 3A), as predicted.

Most crossbills are nomadic over large areas (Newton 1972; Benkman 1987b); therefore, local mismatches are common. For example, the ponderosa pine crossbill (type 2 of Groth 1993) is common in Rocky Mountain ponderosa pine (*Pinus ponderosa* ssp. *scopulorum*) forests and has a bill and a groove in its palate for husking seeds (husking groove) that approximate the optima for foraging on these pines (C. W. Benkman, unpublished data). However, this crossbill is also common in ponderosa pine (*P. ponderosa* ssp. *ponderosa*) forests farther west where its bill and palate groove are smaller than the optima (Benkman 1993a). Presumably ponderosa pine crossbills move between the different subspecies of ponderosa pine (and other conifers), but their morphology matches one conifer precisely and others less well.

Larger areas of lodgepole pine, such as the Cypress Hills and the South Hills (approximately 80 and 90 km<sup>2</sup> of lodgepole pine, respectively), allow crossbills to become resident. Here, coevolution between the resident crossbill and lodgepole pine results in divergent selection between crossbills in these areas and nearby areas with *Tamiasciurus*. As in other areas where crossbills specialize on a single resource, crossbills are likely well matched to their food resource. In these coevolutionary hot spots populations may be cleaved off as new species, thereby decreasing the remaining mosaic of the original species. Divergent selection, therefore, is a double-edged sword. Divergent selection is critical in creating a selection mosaic but erodes the selection mosaic if it promotes reproductive isolation and speciation (see also McPeck 1996). This also shows that part of the adaptive landscape on which crossbills evolve (Benkman 1993a) is dynamic and driven by crossbills (fig. 10).

#### Replicate and Rapid Coevolution

Coevolution has been recent and rapid. Crossbills and lodgepole pine probably coevolved for only the past 6,800 yr in the Cypress Hills. Allozyme studies of lodgepole pine (Wheeler and Guries 1982a; Dancik and Yeh 1983) are consistent with the hypothesis that lodgepole pine, widespread in the western United States near the end of the Pleistocene (Critchfield 1985), spread from the northern Rocky Mountains and colonized the Cypress Hills after glaciers retreated 12,000 yr ago (see Thompson and Kuijt 1976). Crossbills likely became resident only in the past 6,800 yr because that is when lodgepole pine became common, as shown by the pollen fossil record from the Cypress Hills (M. Sauchyn, personal communication, 1994; see also MacDonald and Cwynar 1985). Similarly, pine was probably too rare to support a population of *Tamiasciurus* prior to 6,800 yr ago. *Tamiasciurus*, however, would not have been able to colonize the Cypress Hills in the past 6,800



**Figure 10:** A schematic of the adaptive landscape for red crossbills (*Loxia curvirostra* complex) in western North America. The two important dimensions of adaptation are bill depth for separating cone scales and husking groove width for husking seeds (Benkman 1993a). The adaptive peaks are indicated by stippled circles; WH = western hemlock; DF = Douglas-fir; PP = ponderosa pine; LP = Rocky Mountain lodgepole pine; C/SH = lodgepole pine in the Cypress Hills and South Hills. Coevolution between crossbills and lodgepole pine has resulted in a new peak (arrow).

yr because extensive grassland steppe has surrounded the Cypress Hills throughout the past 10,000 yr (Ritchie 1976; Thompson and Kuijt 1976; see also Barnosky 1989) and *Tamiasciurus* avoid crossing open habitat (see, e.g., Benkman et al. 1984). Unfortunately, opportunities for further coevolution between crossbills and lodgepole pine have been extinguished with the introduction of *Tamiasciurus* in 1950. Crossbills are now uncommon on the Cypress Hills (C. W. Benkman, personal observation), and the population represented by the distinct red crossbills collected in 1948 by Godfrey (1950) may be extinct.

Lodgepole pine has been in the South Hills longer than in the Cypress Hills. Macrofossils of lodgepole pine date back at least 12,400 yr (Davis et al. 1986). How long *Tamiasciurus* have been absent, if they were ever present, is less certain. Lodgepole pine forests in the South Hills were likely connected to lodgepole pine forests in adjacent ranges over 10,000 yr ago but have been isolated since (Wells 1983; O. K. Davis, personal communication, 1997; see also Bright 1966). If so, *Tamiasciurus* have been absent from the South Hills for <10,000 yr.

Six to ten thousand years might seem like a short time, especially for lodgepole pine, to evolve substantial differences. However, rapid and extensive evolution of quantitative traits, including that of cone structure, has oc-

curred in other populations of lodgepole pine (Aitken and Libby 1994; Xie and Ying 1996). Moreover, many studies show that rapid rates of evolution are common in changing or novel environments (e.g., Endler 1986; Lister 1989; Carroll and Boyd 1992; Grant and Grant 1993, 1995; Cody and Overton 1996; Carroll et al. 1997; Losos et al. 1997).

Perhaps the similarity of the crossbills and lodgepole pine in the South Hills and Cypress Hills is the result of the colonization of, for example, the more recently forested Cypress Hills by crossbills and pine from the South Hills rather than an example of convergence. This scenario is doubtful, given that genetic studies indicate that lodgepole pine in the Cypress Hills are derived from a source well north of the South Hills (Wheeler and Guries 1982a). If, as is likely, cone evolution in each area was gradual from a Rocky Mountain-like ancestor, then gradual and convergent evolution of resident crossbill populations in each area is the most plausible scenario. This, however, should be tested with genetic studies.

Although there is convergence in structure between the cones and bills in the Cypress Hills and South Hills (figs. 2, 3, 7), there are differences between the two areas. The bill size and shape differences (fig. 7) are difficult to evaluate because measurements of the Cypress Hills crossbills were made on museum specimens, whereas those from the South Hills were made on live individuals. The more extreme cone defenses in the South Hills than in the Cypress Hills (fig. 3), however, are probably real and deserve consideration. Several explanations are possible. First, lodgepole pine in the South Hills may have been derived from pine with better crossbill-defended cones than those ancestral to the Cypress Hills. This is unlikely because of the uniformity of cones throughout the Rocky Mountains from southern Canada to Colorado (fig. 3). Second, evolution in the absence of *Tamiasciurus* may have occurred for a longer time in the South Hills than in the Cypress Hills. This idea is consistent with the history of the two regions, although it is far from certain. Third, the crossbill population in the South Hills may have been more stable over time and exerted more continuous selection than in the Cypress Hills. For example, fires burned most if not all of the pine forests in the Cypress Hills, and hundreds of kilometers of surrounding prairie, in 1886 and 1889 (Newsome and Dix 1968). This occurrence would have eliminated resident crossbills from the Cypress Hills; the distinct crossbills collected in 1948 by Godfrey (1950) presumably evolved subsequent to these fires. In contrast, one or two fires are much less likely to burn most of the pine stands in the South Hills than in the Cypress Hills because forests in the South Hills are more fragmented by deep ravines and treeless expanses than in the Cypress Hills.

Whether the coevolutionary arms race has stabilized or will continue in the South Hills is unknown. Coevolution

might stabilize for several reasons (Holt and Hochberg 1997). One reason is that there are trade-offs so that costs eventually outweigh benefits. Based on the estimated costs and benefits in terms of individual cones (fig. 6), cones should continue to evolve in response to selection from crossbills. However, this point assumes that the only costs relate to individual cones, yet other costs may be involved. Heavier cones, for example, might cause the slender branches to break or bend so that photosynthesis is compromised. Without more complete measures of trade-offs, I am unable to differentiate between a coevolutionary arms race that is ongoing versus one that has stabilized.

In sum, crossbills and lodgepole pine coevolve rapidly and consistently when a range lacks *Tamiasciurus* and contains about 80 km<sup>2</sup> or more of lodgepole pine. That is, coevolution is repeated or replicated given these two conditions. This replicate coevolution is analogous to replicate adaptive radiations in certain fish in postglacial lakes (Schluter and McPhail 1993) and *Anolis* lizards in the Greater Antilles (Losos 1992; Losos et al. 1998).

#### Divergent Selection and Speciation

Coevolution between crossbills and lodgepole pine causes divergent, multifarious selection between crossbills in different parts of their range, which has resulted in distinct bill morphologies and differences in call notes (fig. 2). Differences in morphology and call notes have been used by Groth (1993) to argue for the recognition of the different call types, including the lodgepole pine crossbill, as distinct species. Differences in call notes are significant because they appear important in positive assortative flocking (crossbills flock year-round, even when breeding; Benkman 1997), which may enhance feeding efficiency via the use of public information and perhaps contribute to reproductive isolation if crossbills chose mates from within flocks (Smith et al. 1999). The Rocky Mountain and South Hills crossbills also likely differ in their tendencies to disperse (e.g., a reduction in dispersal by South Hills crossbills) and in their breeding seasons.

Divergent selection should favor positive assortative mating (reinforcement) if, assuming polygenic inheritance of bill size and shape, intermediate morphologies are disadvantaged at foraging on lodgepole pine in either the Rocky Mountains or the South Hills. The foraging data suggest a depression in performance and potentially fitness (Benkman and Miller 1996) for intermediate morphologies (fig. 9). Positive assortative mating, in turn, should lead to genetic differences. So far, however, genetic studies have not revealed any differences. No nucleotide differences were found between two South Hills crossbills and two lodgepole pine crossbills in a 717-bp segment of the mitochondrial DNA control region; one nucleotide inser-

tion difference was found between these four crossbills and two other lodgepole pine crossbills (Questiau et al. 1999). This result is not surprising, given the recency of possible separation and that gene flow may still be occurring. Studies of mating behavior are needed to determine the extent of reproductive isolation.

#### Do *Tamiasciurus* Influence the Evolutionary Trajectories of Other Species?

*Tamiasciurus* are important predators on many large-seeded pines in western North America, including some that rely on corvids for seed dispersal (Benkman et al. 1984; Benkman 1995a, 1995b). As with crossbills, *Tamiasciurus* can outcompete corvids for seeds (Benkman et al. 1984). In contrast to crossbills, corvids such as Clark's nutcrackers (*Nucifraga columbiana*) are seed dispersers and mutualists with some large-seeded (>90 mg) pines (Vander Wall and Balda 1977; Tomback 1978; Tomback and Linhart 1990); crossbills specialize on conifers with <50-mg seeds. Moreover, some of the cone traits preferred by nutcrackers and *Tamiasciurus* are the same (Benkman 1995a). That is, both nutcrackers (see, e.g., Christensen et al. 1991) and *Tamiasciurus* preferentially harvest cones with a higher ratio of seed mass to cone mass. However, antagonistic selection occurs on pinecone structure because nutcrackers are mutualists (i.e., results in selection for higher ratio of seed mass to cone mass) and *Tamiasciurus* are predators (i.e., selection for smaller ratio of seed mass to cone mass).

*Tamiasciurus* are common in forested habitats, and here selection by *Tamiasciurus* apparently overwhelms counterselection by corvids favoring a smaller ratio of seed mass to cone mass. Consequently, large-seeded pines in forested habitats lack obvious adaptations for corvid seed dispersal (Benkman 1995b). Instead, these pines rely on wind dispersal or secondary seed dispersal by mammals once the seeds reach the ground (see, e.g., Vander Wall 1992). Where *Tamiasciurus* are uncommon or absent, selection by corvids favors an increase in the ratio of seed mass to cone mass, which facilitates seed harvest by corvids. *Tamiasciurus*, therefore, limit the evolution of effective bird dispersal to pines in more open habitats (Benkman 1995a, 1995b).

This sets up a selection mosaic with pines relying on corvids for seed dispersal and having cone traits that ease the harvest of the seeds where *Tamiasciurus* are absent, but not in forests where *Tamiasciurus* are common. Limber pine (*Pinus flexilis*), for example, relies on Clark's nutcrackers for seed dispersal (Lanner and Vander Wall 1980; Benkman et al. 1984) and occupies forests and more open habitats with and without *Tamiasciurus*, respectively (Benkman et al. 1984). In the Rocky Mountains where *Tamiasciurus* are common, limber pinecones are better

matched for defending against *Tamiasciurus* but are relatively poorly adapted for bird dispersal even in local areas without *Tamiasciurus* (Benkman 1995a). In contrast, limber pine in the Great Basin, where *Tamiasciurus* are absent, have cones convergent with more classic bird-dispersed pines and presumably are much better adapted for bird dispersal (Benkman 1995a). Thus, the presence of *Tamiasciurus* defines the evolutionary trajectories of other conifer seed-eating birds and pines.

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